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Mother Nature's Tolerant Ways:

Why non-genetic inheritance has nothing to do with evolution

Abstract

Recently a number of theorists have suggested that evolution can use non-genetic or environmental inheritance to pass on adaptations (e.g. Mamei, 2004). Furthermore, it has been suggested that non-genetic, or environmental factors, can play a central role in the process of evolution that is not captured by the neo-Darwinian view which places natural selection centre-stage (e.g. Odling-Smee, Laland & Feldman, 2003). In this paper we present and clarify neo-Darwinian theory and then take issue with the notions of contemporary gene-centred selection and inheritance that non-genetic inheritance theorists have used. We claim that they have misunderstood the distinction and relationship between intrinsic and extrinsic inheritance and we clarify this with a number of examples from the behavioural and biological sciences. According to this analysis there is no such thing as biologically independent non-genetic inheritance, all extrinsic inheritance is a consequence of traits and dispositions that are intrinsic to an organism and intrinsic design can only be explained through neo-Darwinism. We point to the implications this view has for current conceptions of cultural evolution.

Key words: Natural selection; Non-genetic inheritance; Evolutionary tolerance

1. Introduction

Recently a number of theorists have argued that the received view of biological evolution is wrong. Their arguments focus around the nature and role of the gene as a unit of selection, a unit of instruction and a unit of inheritance. All of these arguments seek to distance themselves from a gene-centred view of evolution and to augment neo-Darwinian theory with other processes and mechanisms that can account for design.

The purpose of this paper is to clarify neo-Darwinian theory and in so doing show behavioural scientists the scope of neo-Darwinism. We believe that recent arguments relying on non-genetic inheritance have significantly underestimated the explanatory resources of neo-Darwinism. We begin with a detailed statement of the received view, framed within a discussion of intrinsic design and using examples from cognitive psychology (sections 2 and 3). We then use this statement as a tool to unpick various assumptions and errors in three forms of the contra-orthodoxy argument – the argument from development, the argument from environmental change, and the argument from extrinsic inheritance. This last argument receives a great deal of attention in order to firmly establish the framework we begin the paper with.

2. The Relationship between Design and the Environment

Imagine that you are to build a robot that has the one function of travelling across a room. A simple solution would be to build a machine with wheels powered by a motor. The machine should readily travel across the floor toward the opposite side of the room, where it will hit a wall and stop.

This machine is not terribly sophisticated as it has no internal control over its movement; its wheels simply keep going until power is lost or an obstacle is met. A more advanced machine would move around obstacles, and turn away from a wall when it meets one. This would require lateral sensors, such that left-side sensors would switch right-side wheels off, and vice versa. With such sensors and wiring the robot could take input from a world of solid objects and, for the most part, move away from them. However, meeting an object head-on would stop the robot so that the intervention of an engineer would be necessary for continued movement.

To solve the problem of head-on encounters more architectural features are required. Such features will add new circuits to the motor control system, perhaps allowing reverse movement for a limited period, perhaps something more complicated. Whatever additions, the aim would be to use the input from head-on encounters to prompt a new behaviour, which in turn would render the robot more independent from the interventions of engineers.

From this we can draw an important lesson. The particular environment encountered is only navigable by our robots if they are designed in a particular way. More precisely, the robots must be prepared for the inputs they receive for these inputs to bring about the functional outcome: the robot's movement across the room. The second robot was not prepared to use the input from its sensors when it encountered an object head-on. As we suggested, the only way to make this input informative was to

change the internal architecture of the robot, and this would prepare the system for such inputs in the future. However, the second robot was prepared to use individual inputs from its left and right sensors (when these did not co-occur), and this made these input patterns informative.

The sensory input devices of this robot would also have to be specialised, only taking a certain sort of input from the world. For example, paddles might be used. When a paddle comes into contact with an object it is depressed and this sends a signal to the appropriate set of wheels instructing them to stop. We can refer to such sensory input devices as domain-specific. For the second robot, the domain-specific inputs that it could use towards fulfilling its function defined its environment. This robot only knew the world through a subset of such inputs; those that its internal architecture prepared it to accept. We could define this subset of inputs as the robot's ecology. That the robot can use this specific ecology is a consequence of its design. Or, to put this point another way, the robot's design defines a potential ecology and a match of the encountered ecology to this potential ecology is necessary for the robot to fulfil its function.

Organic life appears designed just as the robots are. This is because organic life appears to produce purposeful functions under certain conditions. Organisms take different inputs from different aspects of the environment and these inputs change various aspects of those organisms. For example, humans (among many other species) take air into lungs. The oxygen in the air is absorbed and oxygenates red blood cells as they flow through the lungs. The oxygen is then transported around the body by the red blood cells and is used up at different sites of metabolic action in the rest of the body. Deoxygenated blood eventually returns, through the circulation of the vascular system, to the lungs where it is re-oxygenated and the cycle continues. Oxygen is crucial in maintaining all of the body's many processes. Other, inert gases can be inputted but they have no such effect. Such gases can displace oxygen or reduce the level of oxygen saturation in the gases entering the lungs and thereby cause the system to fall into disarray, but note that this is not a systematic effect, but rather a systemically catastrophic one. The pulmonary system is prepared for the input of oxygen, and only oxygen.

Robots and organisms, by dint of their internal design, are able to utilize specific inputs. In the case of robots the design results from decisions made by engineers. In the case of organisms the design results from the operation of natural selection, the blind algorithmic process that Darwin first described in 1859.

Organisms are more complicated than robots, but not simply because they exhibit many more features (which is currently true) but because they also inherit their design features. Genes are the units of this inheritance. Although genes do not directly produce all the features of an organism, they either direct the assembly of amino acids into polypeptides or they control the production of polypeptides and other bio-molecules indirectly as part of an organised decoding system. Polypeptides fold into mature proteins which in turn are organised to form all of the various systems that constitute an organism. Not all of these processes are understood yet, but the central role for DNA has been well established ever since classic experiments involving the phenomena of bacterial transformation (Avery, MacLeod & McCarty, 1944) and bacteriophage replication (Hershey & Chase, 1952) confirmed that DNA was the genetic material.

Modern evolutionary theory sees genes as the fundamental level of analysis (Dawkins, 1976) because genes are ultimately affected by the success of the traits they build. A trait that is selected against is a trait that fails to use inputs from the environment in such a way as to further the survival and, crucially, reproductive success of the organism bearing it. The genes for this trait will not make it into the next generation, and the source of this intrinsic design feature will be lost.

Genes are also the principal source of new intrinsic design in organisms, having the same functional role as the engineers who alter the design of robots in order to meet challenges from the environment. But this role is fulfilled with rather greater conservatism in that alterations are made in series to a lineage of organisms and with a higher probability, after selection, associated with alterations of small effect. Gene mutations can effect change in two main ways: 1. by altering gene expression levels or 2. by altering gene sequence and hence function (for a recent discussion of adaptive genetic change see Nachman, 2005). Individual mutations may be harmful, but the accumulation of favourable mutations ultimately produces new phenotypic features. It is through these means that novel design is added to a species and it is through this method that changes in environments can be countered such that organisms are newly equipped to process novel inputs meaningfully.

Unlike designing robots there is no pre-specified set of functions that an organism must have. What counts most simply for an organism is its ability to reproduce and pass its design features, its traits, onto the next generation. Organisms inherit design from their previous generations and this design allows them to process inputs that they are prepared for. Environmental change, which is often detrimental to survival, is countered by beneficial mutations (or shuffling of existing mutations through recombination). Such mutations are beneficial because they increase the probability of survival or the fecundity of organisms relative to conspecifics. So natural selection is the consequence of intrinsic design features meshing more or less well with an environment, and, for each step in this process, this is ultimately a chance occurrence. Only those designs that allow an organism to survive and reproduce in an environment will be selected. This means that only those intrinsic features of an organism that in some way represent the external world and deliver a useful response will be selected for and can be considered adaptations.

3. Day-to-Day Changes and Cognition

In our description of natural selection we discussed environmental change and the requirement to alter intrinsic design. We used the robot examples to demonstrate that certain environmental problems require new phenotypic features to solve them and that this means new intrinsic architecture. However, we are aware that many aspects of the day-to-day environment change and that organisms seem able to deal with this. This is not a challenge to the view we espouse.

Very simple organisms, like our simple robots, can deal with change just so long as that change is represented in their intrinsic design. So, only some change is relevant to such organisms, while other changes can go unnoticed. For example, our second robot had lateral sensors to detect objects and we showed how these sensors could control movement in an appropriate way. The design

represents a certain form of possible environmental change. If there is an object on the left of the robot, it will be able to move right to avoid it. The robot might exist in a room of fixed obstacles for a period of time, but if it were moved to a new room with new obstacles the same conditional architecture would allow it to navigate and deal with such change. Equally, if a new obstacle were to be placed in the robot's usual room it could cope. If this obstacle was another robot that could move around, the robot could still move away from it.

Evolutionary psychology analyses behaviour in terms of possible adapted functionality and through such functional decompositions begins to describe the kinds of computations that a brain must run in order to deliver behaviour. These computations, as with our robots', can be understood as conditional reasoning mechanisms that take some input p , and produce some output q such that $p \rightarrow q$. Under this description, p represents a class of inputs that arise within a specific adaptive problem domain. The computational mechanism that accepts p and produces the appropriate q , which represents a class of adaptive behavioural responses to p , can be thought of as a module (see Samuels, 1998, for a discussion). This module will contain some content, in the form of a statistical composite of representations of p , such that there is a 'concept' of p , and some specific operations for delivering q . Note that under this description, no such thing as a domain-general problem-solving device could exist for there is no such thing as a domain-general problem that could lead to the selection of a particular $p \rightarrow q$ device (for a discussion of degrees of domain generality see Atkinson and Wheeler, 2004). Adaptive problems are about very specific things such as food acquisition, mating interactions, social exchange, etc. What is more, we know from work in artificial intelligence that robots with domain-general mechanisms find complex problem spaces, of the sort faced by most organisms, computationally intractable. Only when the computational architecture is divided into domain-specific frames, that contain appropriate content and computational processes, do robots succeed in complex spaces (Tooby & Cosmides, 1992; Fodor, 2000).

Cosmides (1989) has provided the now classic empirical example of this approach with her work on social reasoning. Cosmides took an extant conditional reasoning paradigm, the Wason Selection Task, which typically produced incorrect responses across a wide variety of participants when presented in an abstract form. Overall in this form fewer than 25% of participants reason correctly, and typically it is lower than this with around 9% of the participants succeeding. Cosmides argued that, given the overwhelming evidence in support of a social origin for much cognition, people might be expected to conditionally reason better when the task is set in a social domain. More specifically, given that social species need to be wary of cheats, people should reason very well about social contract violations even if they follow the same conditional formalism as the abstract task. This is indeed what Cosmides found and she produced a huge facilitation effect by packaging the same logical problem in a social contract scenario. This effect has proved to be cross-culturally robust (Sugiyama, Tooby & Cosmides, 2002) and has neurological evidence to support the proposed cognitive architecture (Stone, Cosmides, Tooby, Kroll & Knight, 2002). Cosmides has clearly provided strong evidence for domain-specific reasoning abilities with her experiments (but see Fodor 2000 for an argument about the possible conflation of the kinds of logic invoked in Cosmides's tasks; also Dickins 2003).

What evolutionary psychology provides is an account of behaviour in terms of internal computational processes that rely in part on stored content. This stored content allows the recognition of input as well as the 'tripping' of appropriate processes that will deliver an output. Traditional cognitive models have had great difficulty in understanding the nature of content, as well as the source of its veridical nature. Natural selection clearly accounts for its veridical nature (see Millikan, 1993, for a related discussion). However, it is clear that for such cognition to work well the organism must find itself within an appropriate environment, where it can receive appropriate inputs and where its outputs make sense.

The evolutionary psychology account extends to learning mechanisms too. Learning mechanisms are sensitive to specific domains (Gallistel, 1999). What is more, to make learning useful it must be constrained. If learning were the outcome of a general associative mechanism, that associated everything with everything, we would know nothing of the world. Instead, we need to selectively associate certain things, things that are important. For example, associating smoke with fire is useful, and so perhaps some order of Humean contingent and temporal regularity rule might be helpful in facilitating such knowledge acquisition, as well as a disposition to attend to certain salient features of the world. The Garcia Effect, which shows that rats will associate taste with nausea but not with unpleasant visual or auditory stimuli, was a conclusive early demonstration of this fact (Garcia & Koelling, 1966), and is further supported by the need to introduce a contingent and salient stimulus in order to train new associations. Without reward or punishment learning cannot be achieved; one requires something to tie the learning to adapted dispositions.

Day-to-day changes in the environment can be dealt with by an organism that is sufficiently prepared to deal with the relevant inputs. This is not an infinite capacity, for it is one that has been designed by natural selection. Evolved cognition, then, can be seen as a set of calibration devices that help to fit an organism to its not-quite static environment. This does not mean that natural selection had great foresight in predicting future change, but, on the contrary, that some change, at the day-to-day scale, is reliable.

4. Arguments against Orthodoxy

What we have discussed so far represents the orthodox view of evolution. However, some theorists complain that this gene-centred view operates on the premise that genes are precise blueprints for an organism, and in so doing it fails to encapsulate the dynamic interaction with the environment that occurs during development. Apparently:

This premise is based on the underlying assumptions that phylogenetic information is somehow encoded in the genes and that in the course of development this information unfolds by way of (a) predetermined maturation or (b) activation by some (usually unspecified) environmental input... This explicitly preformationist view virtually ignores the role of developmental processes in the realization of phenotypic characters or traits. It assumes that development is internally determined, set on course at conception and specified by genetic programs designed and selected over evolutionary time. (Lickliter and Honeycutt, 2002: 821)

Lickliter and Honeycutt continue their paper with an argument defending a role for extrinsic factors in evolution. They note that gene expression can be switched on or off by a number of internal and external signals “including such non obvious factors as the light-dark cycle... and tactile stimulation” (p. 823) and they discuss how movement is essential for bone development in birds during their chick phase.

Arguments of this sort amount to nothing more than arguments by suggestion. In Lickliter and Honeycutt’s case the suggestion is that the orthodox view has adopted some sort of essentialism and believes genes to contain the instructions and resources for building an entire organism. However, the evidence they present is fully in line with an orthodox and non-essentialist explanation, for Lickliter and Honeycutt’s entire argument rests on a misinterpretation of evolved design.

As discussed, natural selection creates design. This design is an intrinsic property of an organism and extrinsic features only make sense in terms of this intrinsic design. Gene mutations have regular effects on phenotypic design. Given this there is no need to claim that genes are the sole authors of that design, just that they are essential and intrinsic. It is well known, for example, that Hox genes (the evolutionarily massively conserved genes involved in the basic body plan) are controlled by species-specific genes, as well as chemical gradients in order to give distinct body shape. What is more, these genes compete for resources to build various aspects of the body and will greedily take over resources if other Hox genes are knocked out, or chemical gradients altered, leading to major dysmorphia and usually death (see Deacon, 1997, for a discussion). What is asserted, purely as a logical consequence of what evolution does, is that for nutritional inputs and for signals from other developing systems etc. to have a systemic effect there must be preparedness for the input. Genes are not only intrinsic features but they are also inherited, and they are consistently brought to each developmental situation, and therefore consistently set the agenda for other inputs. But this must not be seen as a compromise. Theorists, such as Lickliter and Honeycutt, have not only failed to understand the orthodoxy, but they have also failed to grasp how an understanding of the intrinsic design features of an organism help us to understand the nature and role of extrinsic environmental features. The role of chemical gradients, light dark cycles and tactile stimulation only make sense in light of intrinsic design and intrinsic inheritance.

Lickliter and Honeycutt represent one unorthodox error. There are others. Recently some theorists have begun to worry about the extrinsic features of organic life in relation not to ontogenetic processes but to evolutionary processes themselves. Odling-Smee, Laland & Feldman (2003), for example, have discussed in detail the phenomenon of niche construction. This is where the actions of an organism change the ecology in which they live to such an extent that it has an effect upon the phenotypic features of that organism.

One example is that of the earthworm. The action of burrowing has altered the consistency, as well as the chemical composition, of the soil in which this species lives. This has led to an increase in the number of plants that grow in the soil, which in turn provides earthworms with more to consume, thus improving their nutritional lot. It has also made the task of moving through the soil less onerous than that originally confronted by earthworm ancestors, for the soil has become more broken up. As a

consequence of this earthworm epidermal and mucus secretion structure has changed over a number of generations.

It is important to be clear about what is happening in the above example, and more generally within niche construction, as well as what is not happening. From the perspective outlined in this paper, earthworms had certain heritable intrinsic features that allowed them to act in certain ways that were adapted in past environments. However, these very actions altered the environment in which they lived to such an extent that new selection pressures were brought to bear upon earthworms. Fortunately, earthworms presented sufficient variation or an appropriate mutational change in their intrinsic structure, to adapt to the new environment. What is more, these intrinsic features, as for previous traits, were heritable. In short, niche construction refers to effects that organisms can have upon the selection pressures that confront them. What is not happening is a new evolutionary process whereby novel inputs are themselves rewiring the intrinsic features of the organism, which is in fact what Odling-Smee et al. claim, for they see niche construction as a neglected process in evolution, running alongside natural selection. This claim amounts to a Lamarckian position, which is biologically implausible. All that Odling-Smee et al. point to can be explained by natural selection (see Dickins, 2005, for a more detailed discussion of Odling-Smee et al.).

Odling-Smee et al. are not the only theorists discussing a role for extrinsic features in evolution. A clearly related discussion is being had by some anthropologists and psychologists about the role of human cultural behaviour in the evolution of humans, and more specifically about the role of memes, a notion first put forward by Dawkins (1976). Memes defy precise definition (see Auger, 2000 for much discussion), but as a broad characterisation they are ideas that are transmitted vertically, horizontally and obliquely and that can be seen as the cultural equivalent of genes. In other words, memes are inherited and selected and, as core components of culture, they have a potentially huge effect upon humans. Cultural practices, for example, could be transmitted that have effects upon the phenotype of those involved, and, over time, this inheritance allows the new phenotype to increase in relative frequency. However, such a situation could only arise in one of two ways:

First, cultural effects could be seen as a form of a niche construction where cultural behaviours alter the intrinsic design of, for example, humans. But, as we argued above, such effects can only be regarded as a case of natural selection, where organismic action has altered the selection pressures confronting that organism or set of organisms. They cannot be understood in terms of cultural inputs directly altering the design of the recipient, without imputing magical and essential properties to those inputs. What is more, the original outputs are the consequence of the intrinsic design of the organism. Given this the second and more moderate way for cultural practices to affect phenotypes is to see culture (or memes) as predicated upon extant intrinsic design.¹

A consequence of the position we have outlined is that cultures cannot truly evolve, in the full biological sense, for they have no independent existence outside of the biologically based behaviours that produce them. As such, any evolutionary story to be told about culture will be a story about the evolution of cultural agents, or more specifically, about the evolution of their cognition. Memes, then, amount to nothing more than a cognitive output, the consequence of a designed system that processes certain inputs in specific ways. That humans can use such outputs as inputs again does not undermine

this point. Under this conception memes have no existence independent of evolved human minds and this leads us to question the explanatory value of this theoretical concept. Interestingly, Dawkins (1991) made a related point about memes when he described them as viruses of the mind, thus conveying the idea that memes fit the system they infect and act informationally. According to Dawkins our cognition has evolved in such a way as to leave us vulnerable to memes that can cause us to act in potentially irrational ways.²

5. The Case For and Against Non-genetic Inheritance

Mameli (2004) has recently contributed a detailed discussion of extrinsic factors and evolutionary process, and it is his argument that shall form the core discussion point for the rest of this paper. Whereas previous criticisms of orthodoxy have looked for a role for factors other than genes, or processes other than natural selection, Mameli has focused upon other forms of inheritance.

Mameli states that the received view within evolutionary biology, that only genes are inherited and that only genetically caused phenotypic variation is selected, is wrong. In his paper he claims that there are other forms of inheritance too, and he argues for ‘intergenerationally stable phenotypic differences due to environmental differences’ (p. 35). Moreover, his argument posits no intrinsic change at all.

According to Mameli (2004), inheritance is about the preservation of similarity. Inheritance mechanisms, therefore, “are all those mechanisms that cause organisms to resemble their parents in phenotypic and/or genetic and/or environmental traits” (p.51). This is immediately problematic, because the orthodox, gene-centred view describes inheritance in terms of relative gene frequencies and these are affected by phenotype-environment interactions. Similarity does not enter into the definition but more critically, those genes that code for beneficial traits are passed on, evincing some order of similarity, while those that are deleterious are not. In other words, the similarity noted in offspring is permitted by natural selection. Similarity is a by-product and not where the real action is. Despite this fundamental difference let us continue with his thesis:

Mameli sees the three types of inheritance – phenotypic, genetic and environmental – as theoretically separable and each with their own real effects in the natural world. To this end he offers the thought experiment of the lucky butterfly.

The lucky butterfly belongs to a species of butterfly that has genetically identical individuals: a species that suffers no genetic variation (often referred to as a clone). The genes of this species build bodies in the same way as genes do in all other species; but any variation in those bodies is brought about by variation in environmental inputs. This species of butterfly, when in caterpillar form, is raised on the leaves of a particular species of plant – let us call this Plant Species 1 (PS1). During this phase the caterpillar imprints on the taste of the leaves and this enables it, when an adult butterfly, to locate more PS1 leaves on which to lay its own eggs. In this way the caterpillars grow in the same environment.

The lucky butterfly suffers a malfunction in its imprinting mechanism such that it accidentally lays its eggs on the leaves of Plant Species 2 (PS2). However, it just so happens that PS2 provides a

better environment than PS1 and the butterflies that emerge from the lucky butterfly's caterpillars are bigger and (in this case) fitter (in a Darwinian sense) than the butterflies arising from a PS1 environment. Because these lucky butterfly progeny have an intact imprinting mechanism their caterpillars are raised on PS2 leaves and gradually the relative number of lucky butterfly's descendants increases.

Mameli is at pains to point out that the malfunction in the imprinting mechanism is not a genetic malfunction, yet the lucky butterfly's descendants have benefited from the inheritance of similarity – in this case, a similar caterpillar phase environment, that of PS2 leaves. It is this kind of effect that Mameli labels as non-genetic inheritance and selection. The claim is that thanks to the imprinting mechanism the plant species environment is an intergenerationally stable developmental factor, of the same order as genes in the received view of evolution, and therefore selection can operate to favour this environmentally caused difference within the clone or species. Intergenerationally stable developmental factors are crucial for they can both cause a beneficial trait and allow it to be passed on into the next generation and beyond.

Under the received view selection changes the relevant gene frequencies, but under Mameli's view selection can also alter the frequency of a particular phenotype by changing the frequency of intergenerationally stable environmental factors. The plant species is the intergenerationally stable environmental factor for the lucky butterfly's progeny and this leads to fitness through a bigger size. We can refer to bigger size, the product of selection, as an adaptation.

Once Mameli has presented the theoretical possibility of non-genetic inheritance he then sets about discussing examples of it in the natural world. He is careful to note that the pure-form non-genetic inheritance of the lucky butterfly example is hypothetical; there is always genetic variance underlying phenotypic traits in the real world. But, this does not preclude the existence of stable environmental factors too.

Mameli lists many examples of which we shall outline only one. Pacific salmon imprint upon the river in which they are born using olfactory cues. This imprinting allows them to return to their natal waterway to breed, and as such this site becomes intergenerationally stable. There is potential Mameli-type selection here too, for some waterways are better for breeding and for the subsequent development of offspring.

Given that Mameli has already redefined inheritance in terms of similarity it is not too surprising that he can then go on to find specific examples of it in the natural world. What is more, these cited examples, as with all the others, are again a form of argument by suggestion. We are given ample evidence of imprinting mechanisms and relata in the natural world and then nudged into the intuition that, because of Mameli's earlier comments, and because, for example some rivers provide better environments for salmon development, the logic of his thesis is correct. This really only amounts to a list of possible premises; the work to connect them in a convincing fashion is left to the lucky butterfly thought experiment, and as we shall demonstrate this has serious flaws.

The imprinting mechanism of the lucky butterfly is a non-genetic inheritance mechanism, under Mameli's scheme, because it produces intergenerational developmental stability. According to Mameli, we can take this argument further. He notes that humans are born into an environment with

stable gravitational qualities that are different from those on other planets. These stable qualities aid in the development of species-specific limbs etc., which is not dissimilar to the ‘evidence’ used by Lickliter and Honeycutt to defend their position. According to Mameli:

It follows that it is partly because both my father and I have been exposed to an acceleration of gravity of roughly 9.8m/s^2 that we have developed similar (normal) legs and similar (normal) walking skills. This means that the acceleration of gravity is an inherited developmental factor for all humans. The causal processes responsible for the fact that, generation after generation, humans remain exposed to an acceleration of gravity of 9.8m/s^2 is an inheritance mechanism for humans, even if it is a mechanism that we get ‘for free’, independently of any biological process. (2004:57)

During this paper we have noted a distinction between qualities, or features that are *intrinsic* and *extrinsic* to an organism. Following from this, intrinsic inheritance is the inheritance of constitutive design features, and extrinsic inheritance is what Mameli seeks to defend. Extrinsic factors that are of relevance to the survival and reproduction of organisms are, like intrinsic features, clearly useful. But for extrinsic factors to be useful to an organism that organism must be designed in such a way as to make use of the extrinsically sourced inputs. In this way, extrinsic features are informative. Intrinsic design features will critically limit what can be processed – it is for this reason that we cannot digest granite or see all of the electromagnetic spectrum. This means that in order to fully appreciate the role of what Mameli terms an intergenerationally stable environmental factor we need to understand the design features of the organism that is capable of utilising this factor. Any external input will only have utility if the system is prepared for that input. Such preparedness is the subject matter for evolutionary theory, as we have shown.

The key element in Mameli’s thought experiment is the imprinting mechanism: the design feature of Mameli’s lucky butterfly that allows it to use the PS1 and PS2 environments. The imprinting mechanism can use inputs from PS1 and PS2 and this means that the imprinting mechanism was prepared for these inputs.³ The imprinting mechanism is clearly an adaptation, in that it affords the choice of a stable and useful environment for caterpillars, allowing them to grow and then reproduce themselves. If it is adaptive (even in this loose sense) then there must be an evolutionary story to tell about the origin and make-up of the imprinting mechanism. What is more, this evolutionary story must become a story about the selection of relevant genes because we know, from Mameli, that the nervous system that produces the imprinting mechanism and behaviour is built from genes. So, at some point in the history of this species there was genetic variation at least in terms of the coding for this aspect of butterfly neurology. At some point in history normal selection pressures have trimmed this genetic variation.

The lucky butterfly thought experiment is now somewhat reduced to a discussion about how a given phenotypic trait, imprinting, operates in the world. This does not exactly undermine Mameli’s argument but it does change the focus from discussion of non-genetic selection and inheritance to a comment that the genes controlling imprinting have produced a mechanism with potentially wide targeting – at least as wide as PS1 and PS2. Furthermore, we should not call the lucky butterfly’s accident a malfunction, for this butterfly has simply revealed the breadth of functionality for the

imprinting mechanism, as afforded by natural selection operating over the relevant genes. A malfunction would see a non-imprinting effect (i.e. no imprinting, or only partial imprinting) or a deleterious imprinting, for example, targeting a toxic plant species. The raw material for evolution by genetic selection, mutation, is different in two ways. First, its effects are intrinsic to the source of design (in this case the imprinting mechanism) and, second, at least in interesting cases, it creates new potential within it (whereas here we are limited by it).

Even though we might see non-genetic selection in the real world, i.e. patterns that are commensurate with the lucky butterfly thought experiment, it is perhaps best regarded not as true selection of features that can be intrinsically inherited, i.e. not as evolution per se, but as what we term *evolutionary tolerance*.⁴ Phenotypic traits, expressed by genes, can have a breadth of functionality that affords a certain amount of slack. This can lead to a favouring of some aspects of that breadth over others. For example, there are many ways in which humans can walk, as seen in differences in gait. Many of these differences are due to other system demands, such as muscular-skeletal composition, body weight, sensitivity of proprioception, etc. Yet other aspects, however, are a consequence of the environment and some surfaces afford better locomotion than others. It is entirely possible that moving to a particular terrain will favour some individuals over those that do not move there. What is extremely unlikely is that a very general phenotypic trait would be selected for, such as a general locomotion device that would deal equally well with all terrains and would allow individuals to fly, walk, run, swim, move up vertical surfaces etc. This is for well-rehearsed reasons (see above), for selection operates on domain-specific problems. Legs allow running and walking, and can aid in swimming and climbing, and that is it. To change the domain in which an adaptation operated, in response to radical changes, would require more fundamental (genetic) rewiring. (And this, in turn, requires sources of genetic variation such as mutation and recombination.) In short, the domain of the adaptive problem sets evolutionary tolerance – sometimes this can be relatively broad and sometimes relatively narrow, but it is never infinite. The lucky butterfly's imprinting mechanism has a tolerance of at least 1 + 1 plant species types, and it is more than likely that there are some specific reasons for this having worked out (such as species similarities between PS1 and PS2) that are also a consequence of evolution operating over genes.⁵

There are some other problems with Mameli's argument.

In contemporary neo-Darwinism, an adaptation is a feature that, in a particular environment and through its selection over other variants during evolutionary time, has afforded the organism some advantage over its competitors lacking this feature. The importance of the environment is emphasised in evolutionary psychology in which mismatches between the environment of evolutionary adaptedness and a particular organismic feature are often invoked to explain seemingly maladapted traits. By emphasising the positive possibility that features may be co-opted for or acquire different functions Mameli (2004) seems to offer a new path for evolution through environmental change. As we have argued, the flexibility displayed by the lucky butterfly and acted on by non-genetic selection in Mameli's example is merely *revealed* functionality inherent in an imprinting mechanism that has undergone previous (genetic) selection. But what of the specific claim that non-genetic selection has produced an adaptation in respect of the lucky butterfly's (and its descendents') larger size?

While a change has occurred in his example, neither the butterfly nor the butterfly's imprinting mechanism has acquired a new function. In respect of the butterfly's larger size, this can be seen to be a *consequence* of the superior growth environment offered by PS2. And, while some (lucky) members of the butterfly clone have found a new growth environment (PS2), this environment must share key features in common with the first (PS1) in order for the imprinting mechanism to latch on.

There is also a more fundamental point. We have just implied that the butterfly's larger size cannot be an adaptation to the PS2 environment in respect of selection between environments; however, it is clearly an adaptive response to this environment. The difference is that the change to a PS2 environment can only cause the butterfly's size increase because of the butterfly's inherently adaptive response. And since this relies on an intrinsic property of the butterfly, it must depend on intrinsic inheritance and selection.

Any adaptation is an adaptation to a particular environment. So, as we have argued above we can say that a change in the environment sets the problem in evolution rather than providing the solution. This idea dovetails with the notion of limited evolutionary tolerance. The account of the lucky butterfly now fits squarely into an unreconstructed neo-Darwinism in which the environment, and variation in it, is clearly recognised as the driver for evolutionary change, change that requires intrinsic (genetic) variation.

6. Conclusions

The purpose of the current paper has been to show that all attempts to argue against the orthodox view, that evolution is a process of selection for intrinsic design that relies upon an intrinsic (genetic) inheritance system, have failed. They have failed because they have misunderstood the core notion of natural selection and design. In order to make this argument we have focused upon many aspects of behavioural design, from a conceptual discussion about robot architectures, through an analysis of some key work in evolutionary cognitive psychology and finally to a discussion of how extragenetic inheritance has been conflated with imprinting and learning. Our ambition has been to show how natural selection can build calibrating organisms that have intrinsic design features that capture day-to-day changes. The ability to deal with such changes is often dealt with by learning theories and we hope to have provided an evolutionary perspective on what that means.

We conclude, more radically, that the claims made for non-genetic selection in general fit into a larger intellectual trend whereby cultural processes are given explanatory primacy over biological phenomena. What the reasons for this are remain obscure, but these positions reflect an ignorance of the philosophical underpinnings of evolutionary theory itself. Like all scientific theories, evolutionary theory adopts a form of naturalism and rejects essentialism. The alternative theories discussed in this paper fail to meet this criterion.

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¹ But note that this does not then rule out subsequent feedback effects, whereby organismic action causes new selection pressures to emerge.

² Dawkins refers to various religious ideas as well as those associated with cults etc. He also interestingly hypothesises an increased vulnerability to infection during the early stages of development, as well as an element of path dependent infection, such that some memetic viruses make it more likely that later ones will thrive.

³ If the imprinting mechanism was not prepared for such inputs (in the sense of ‘prepared’ already introduced) then how are we to account for its ability to deal with either PS1 or PS2? There are only two possible alternatives: (1) that the imprinting mechanism is in fact a domain-general learning mechanism or (2) that the inputs from PS1 and PS2 somehow carry content that redesigns the intrinsic features of the butterflies. We have discussed reasons for rejecting (1) earlier in the paper. If we were to explore (2) it will either reduce to a state change argument, and therefore it will not amount to a suggestion of systemic rewiring, or it will violate the principles of evolutionary theory by adopting a form of essentialism.

⁴ Dawkins’ discussion of our vulnerability to particular memes might be reconstrued in light of the concept of evolutionary tolerance and seen as a cost of evolved cognitive tolerance.

⁵ It is possible that evolution in PS2 may form part of a more complex account of why the lucky butterfly was lucky, but this does not negate the point made here.